THE MORPHOLOGY OF THE HEAD OF THE HAWFINCH
(COCCOTHRAUSTES COCCOTHRAUSTES),
WITH SPECIAL REFERENCE TO THE MYOLOGY OF THE JAW

BY

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By R. W. SIMS

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SYNOPSIS

The ability of the Hawfinch, *Coccothraustes coccothraustes*, to crack open the stones of cherries, damsons and olives in order to feed on the kernels is generally well known, but the modifications which are present in the structure of the head and enable this comparatively small bird to perform such a feat have apparently received little attention. The method employed by *C. coccothraustes* to crack open the fruit stones is noteworthy because each stone is held between the mandibles and is broken solely by the force applied by the jaw muscles, and not by any " artifice " such as that employed by the thrush to smash snail shells, or the woodpecker to split almond stones. The behaviour of the bird when feeding on fruit stone kernels appears to follow a definite pattern. The bird usually selects fallen fruit apparently discarding the soft parts. Observations and photographs show that a cherry stone is positioned in the mouth by the combined movements of the head and tongue until it is held lengthways between the mandibles at the back of the horny palate of the mouth with the suture of the stone lying in the median sagittal plane of the head. A quick snap of the jaw and the shell is neatly cracked along the suture or " seam ". The halves of the shell are rejected and the kernel is swallowed whole, usually without being crushed. Experiments on breaking open cherry and olive stones (given in detail in the appendix) show that pressures in the region of about 100 lb. are required to perform this feat !

The purpose of this paper is to show how the head of *C. coccothraustes* is adapted to apply and withstand such forces by describing some aspects of the morphology of the head, namely, of the horny bill, or rhamphotheca, the skull and the jaw muscles.

MATERIALS

This study is based on specimens of *C. coccothraustes* collected in Great Britain. The material consists of two adults and two juvenile male specimens preserved in spirit in the National Collection, one head, sex unknown, supplied by Mr. G. R. Mountfort, and several skeletons in the National Collection. In most of the osteological material the rhamphothecae, which can only be removed with difficulty, were intact. The heads of two spirit specimens were dissected completely during the course of the investigation. The head of a spirit specimen of a Brambling, *Fringilla montifringilla*, was also dissected, and reference was made to the series of skulls of the Chaffinch, *Fringilla coelebs*, in the National Collection.

ACKNOWLEDGMENTS

I am indebted to Mr. Guy Mountfort for suggesting this investigation. The work was originally undertaken in order to answer some of the points raised by him in the preparation of his monograph of the Hawfinch. The scope of this study was subsequently enlarged. I am obliged to Mr. H. L. Cox and his colleagues of the National Physical Laboratory, and Mr. D. Welbourn of Cambridge, for providing me with the interesting data which form the appendix to this paper; and to Dr. J. Wahrman of the Hebrew University, Jerusalem, for a supply of fresh olives for the crushing tests. I also wish to thank my colleagues in the British Museum (Natural History) for reading the MS. and for providing many helpful criticisms.

HISTORICAL NOTE

References to the general anatomy of the head of *C. coccothraustes* are remarkably few and are confined mainly to the consideration of characters of the skull as an aid to classification, or less frequently to its architecture. The skull with its high degree of ossification particularly impressed W. K. Parker (1879) by what he called "its ridgy strength" when he described some aspects of the anatomy of the skull in his systematic work on the structure of the palates of passerine birds. At the beginning of the section on *C. coccothraustes* he pointed out that most of the differences between the skull of this species and those of other members of the Fringillidae were of little phylogenetic importance because the modifications in the skull of *C. coccothraustes* were for "mechanical purposes". Nevertheless, Bowdler Sharpe (1888) used many of these modifications "for convenience" to separate what he termed the Coccothraustinae from the buntings and true finches.

The peculiarities of the horny bill or rhamphotheca were noted very briefly by Pycraft (1905), and his observations were occasionally referred to by subsequent workers. Nothing new was recorded on the horny bill until Sushkin (1925) described similar modifications in the bill of the Evening Grosbeak, *Hesperiphona vespertina*.

He concluded that they were essentially the same although purely adaptive characteristics. He agreed with W. K. Parker that most of the peculiarities of the skull were adaptive features, but believed that only one character of the bony palate was of systematic significance, and on that he regarded the Evening Grosbeak as a member of a sub-family containing the Old World hawfinches.

Later references are confined almost entirely to remarks in papers dealing with the mechanical structure of bird skulls, for example those by N. G. von Lebedinsky (1921) and von Kripp (1933*a*). The latter author showed that the skull was structurally stronger than that of a harrier.

The literature appears to contain few references to the myology of *C. coccothraustes*, so an account of the musculature of the jaw is given in this present paper. The nomenclature adopted is that proposed by Lakjer (1926) in his comparative work on the *Sauropsida*.

DESCRIPTION

1. *Rhamphotheca*

The rhamphotheca of birds is derived from the malpighian layer of the epidermis. In most birds it is seldom more than a thin sheath which is readily detached from a dried skull, but in *C. coccothraustes* parts of it inside the mouth are greatly thickened and enlarged. In the palatal region (Text-fig. 1*a*) it forms a longitudinally striated thick pad partly divided by a longitudinal median depression. This thickened area extends from the anterior border of the palatine bones over the posterior third of the premaxillae. The anterior two-thirds of the premaxillae are covered by the remainder of the horny palate which is strengthened by one median and a pair of lateral ridges. The grooves formed between the lateral ridges and the edges of the upper mandible accommodate the edges of the lower mandible. On the lower jaw (Text-fig. 1*b*) the horny sheath is thickened to form two large bosses which lie

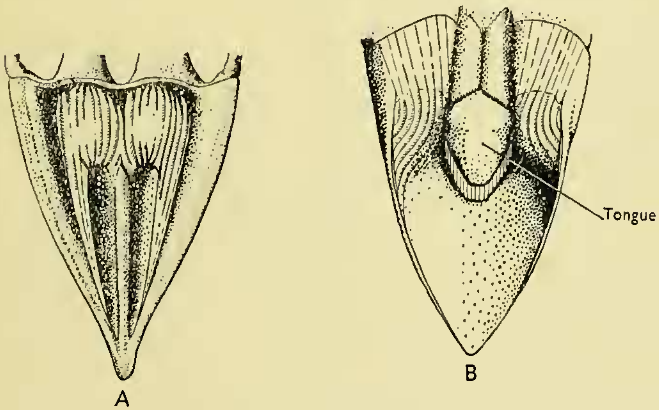

FIG. 1. ***Coccothraustes coccothraustes.*** The oral surfaces of the rhamphotheca showing the striated pads. A, Upper jaw; B, Lower jaw with the anterior of the tongue *in situ*.

immediately over the posterior parts of the dentary bones which are themselves specially thickened in this area. The bosses are striated, but the striations being curved more or less follow the contours. The depression between the two bosses accommodates the tongue. The tip of the tongue is broadly cuneiform in shape and lies flush with the anterior surfaces of the lateral bosses.

2. *Skull*

The principle modifications of the skull which appear to be connected with the ability of *C. coccothraustes* to exert a great force with its jaw muscles can be summarised as follows :

In the first place the whole skull is strengthened by a greater ossification than is usually found in most fringilline species. An indication of the extent of ossification as determined by weight, is given in a later section.

Von Kripp (1933*a*) described how the architecture of the skull is suited to withstand stress and strain. Viewed laterally the outline of the skull approximates to one horn of a crescent, the dorsal profile being convex and the central one concave (Text-fig. 2*a*). The concave ventral surface is strengthened by a system of struts formed by a massive pyterygoid-quadrate-zygoma system. The anterior part of the head is further strengthened by the heavily ossified nasal and interorbital septa. These elements play an important role in the rigidity of the skull for their function is analogous to that of the vertical component of an I-shaped girder.

In the skulls of many birds the whole of the upper mandible is hinged to the cranium, but in *C. coccothraustes* it is rigidly fixed. The suture between the frontal and nasal bones, where the hinge is usually located, is obliterated ; the nasal and the interorbital septa form what is functionally a continuous vertical wall ; and the palatines are ankylosed with the rostrum and vomer which form most of the base of that wall.

The fixity of the upper mandible also may be associated with the nature of the relationship between the cranial head of the quadrate and the surrounding structures in the otic region of the skull. The quadrate is joined to the palatine by the pterygoid and to the upper mandible by the zygoma, and owing to the immobility of the upper mandible the quadrate is held firmly by these bones. The absence of movement together with the great crushing strain imposed on the quadrate by the lower jaw has resulted in the squamosal and opisthotic facets in the otic region extending partly around and in close contact with the small squamosal and opisthotic heads of the quadrate. The extension of the area of contact between the quadrate and the cranium is functionally possible only because the quadrate is held firmly by the pterygoid and the zygoma. The increased area of contact provides a strong base for the quadrate which in its capacity as the fulcrum of the lower jaw experiences great pressures when hard food, such as fruit stones, are cracked.

The great pressures have also influenced the nature of the quadrate which is very massive. Moreover, a powerful muscle, M. Quadrato-mandibularis, originates from its orbital process, and the inclusion of the muscle as an important member of the

Adductor Group has no doubt contributed towards the massive development of this bone.

The post-orbital process of the squamosal is unusually large and this feature may be correlated with the powerful muscle, the pars medius of the M. mandibulae externus, which has a tendinous origin on it. The pars medius is inserted into the

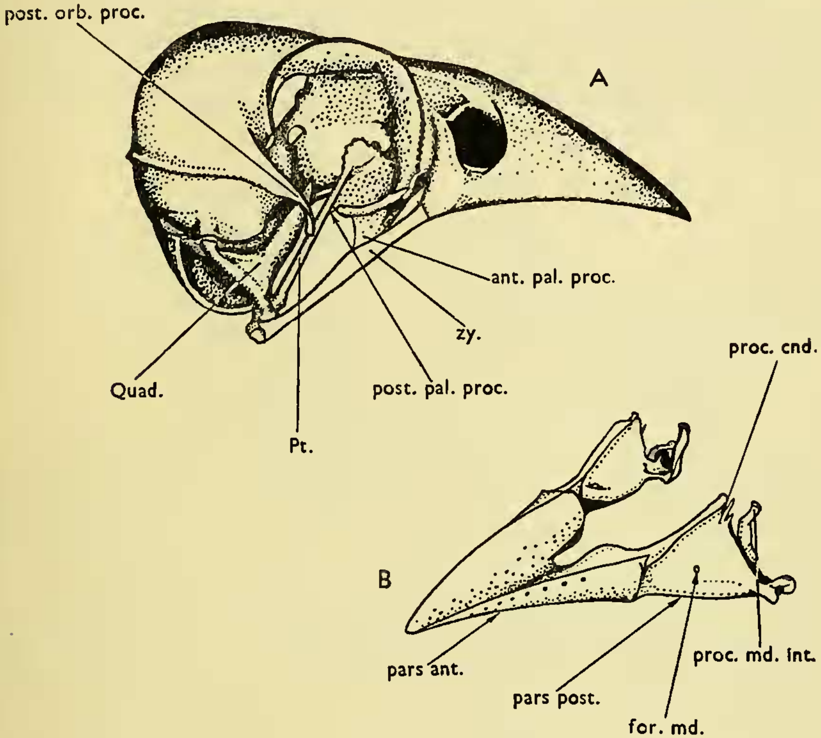

FIG. 2. ***Coccothraustes coccothraustes.*** A, cranium and upper jaw, lateral view from the right side. B, Lower jaw. *Ant. pal. proc.*, anterior process of the palatine ; *for. md.*, foramen mandibularis ; *pars. ant.*, anterior part of the lower jaw (dentary) ; *pars. post.*, posterior part of the lower jaw ; *post. orb. proc.*, post-orbital process of the squamosal ; *post. pal. proc.*, posterior process of the palatine ; *proc. cnd.*, processus coronoideus ; *proc. md. int.*, processus mandibulae internus (articular) ; *pt.*, pterygoid ; *quad.*, quadrate ; *zy.*, zygoma (quadrato-jugal and jugal).

lateral surface of the processus coronoideus, but the modifications associated with this will be discussed later.

Dislocation of the lower jaw from the quadrate during the contraction of the powerful jaw muscles is prevented by a ligament which extends from the zygoma to the posterior surface of the processus mandibulae internus, passing over the posterior surface of the distal end of the quadrate. This ligament has two centres of ossification; one forms a large sesamoid which lies close to, and posterior to, the articulation of the jaw; the other is smaller and lies more laterally near the attachment of the ligament to the zygoma.

The lower jaw, like the remainder of the skull, is massive and ossified to the extent that the foramen mandibularis, usually a large opening, is reduced to a size that permits only the passage of a branch of the trigeminal nerve (Text fig. *2b*).

The anterior part of the lower jaw is strengthened by an inward expansion and union of the paired dentaries, the long symphysis forming a bony shelf. Postero-mesially the dentaries are greatly thickened to serve as strong foundations for the heavy bosses of the rhamphotheca.

3. *Myology of the Jaw*

The muscles involved in the movement of the jaws of birds form four functional groups:

(a) The Adductor Group.
(b) The Constrictor Group.
(c) The Protractor Group.
(d) The Retractor Group.

The Adductor Group raises the lower jaw, the Constrictor Group depresses it; the Protractor Group raises the upper mandible and the Retractor Group lowers it. In *C. coccothraustes* the upper mandible is not hinged on the cranium, as already mentioned, and the muscles of the Protractor Group which persist are functionless, while the muscles of the Retractor Group assist in the elevation of the lower jaw and are dealt with here as members of the Adductor Group.

The Constrictor Group and the Protractor Group in *C. coccothraustes* each consists of only one paired muscle and therefore neither *in sensu stricto* can be considered as a "group". Nevertheless, the term has been used here for convenience in both cases.

I The Adductor Group

The Adductor Group, which raises the lower jaw, is the largest of the three groups. This assemblage in *C. coccothraustes* may be further divided into two clearly marked functional units, one acting from the top and back of the cranium and the other acting from the orbital walls and their vicinity. The muscles of the former are inserted in the ramus of the lower jaw near the superior (dorsal) and the posterior margin of the coronoid elevation. Functionally, this is the more important unit and consists of the Ms. Adductor mandibulae and the M. Quadrato-mandibularis. The other muscles of the Adductor Group, the M. Pterygoideus and the M. Ethmo-mandibularis, are inserted near the inferior (ventral) margin of the ramus of the lower jaw.

Description of the Adductor Group

M. ADUCTOR MANDIBULAE EXTERNUS (Text-fig. 3)

(1) Pars superficialis

The rostral part is fan-like and arises from the cranium over most of the anterior half of the frontal. The area of attachment is confined anteriorally and mesially by the frontal crest, and laterally by the flattened rim of the orbit. The fibres pass forwards and downwards between the post-orbital process of the squamosal

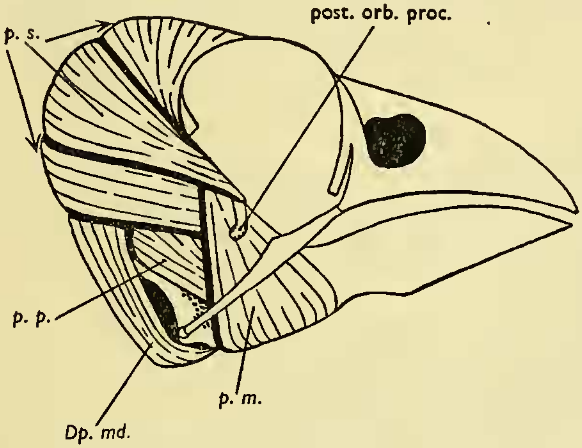

Fig. 3. ***Coccothraustes coccothraustes.*** Diagrammatic view of the right side of the head showing the external jaw muscles. *p.m.*, *p.p.*, *p.s.*, partes medius, profundus, superficialis of the M. Adductor mandibulae externus; *Dp. md.*, M. Depressor mandibulae.

and the rim of the orbit. The fibres converge becoming more tendinous and are inserted at the apex of the processus coronoideus of the lower jaw. The main part extends over the posterior half of the frontal; it is bounded by the rostral part in front and the transverse post-frontal crest behind, and extends inwards to the meso-frontal crest. The converging fibres are directed more forwards than those of the previous part and pass over its aponeurosis and the post-orbital process of the squamosal. The head is inserted in the pars posterior of the lower jaw laterally to the head of the rostral part at the apex of the processus coronoideus. The caudal part arises from that area of the cranium bounded by the transverse post-frontal crest in front and the transverse crest on the posterior part of the squamosal and the parietal. (Mesially the two prominences converge and form a triangular area of attachment). The fibres passing more forwards than downwards become more tendinous as they converge; they are inserted somewhat laterally in the posterior margin of the processus coronoideus. This part is similar in size to the other two but it differs in that the converging fibres pass under both the distal part of the post-orbital process of the squamosal and the ascending fibres of the pars medius (see below).

(2) PARS PROFUNDA

The pars profunda arises from the cranium on the anterior surface of the supra-meatal ridge of the squamosal and in the concavity in the otic region between the cranium and the quadrate, also to the neck of the quadrate. This muscle is very tendinous throughout although it is inclined to be more fleshy in the part occupying the concavity in the otic region. It is inserted in the ramus of the lower jaw ventrally to the site of insertion of the pars superficialis, that is, about half-way along the outer edge of the posterior margin of the processus coronoideus. Some of the fibres and the dense fascia surrounding the muscle coalesce with those of the pars superficialis.

(3) PARS MEDIUS

The pars medius is a fan-like muscle with a tendinous origin on the ventral surface of the post-orbital process of the squamosal. The fibres pass downwards and become more fleshy as they diverge. The muscle is inserted over most of the lateral surface of the processus coronoideus of the lower jaw.

M. ADDUCTOR MANDIBULAE POSTERIOR (Text-fig. 4)

The M. adductor mandibulae posterior arises from the posterior wall of the orbit, namely, from the alisphenoid outside the latero-ventral margin of the fossa in the orbital wall. Mesially there is a thin bony partition which separates the muscle from the M. Pseudotemporalis (see below), and laterally another thin bony prominence extends down from the rim of the orbit and separates the muscle from the descending fibres of the pars superficialis. The muscle is short and very tendinous. It is inserted in the mesial surface of the processus coronoideus near the upper half of the posterior margin. There are a few tough ligamentous strands extending the whole length of the muscle and these are inserted in the small dorsally directed conical process of the mesial surface of the processus coronoideus near the posterior margin.

M. ADDUCTOR MANDIBULAE INTERNUS (M. PSEUDOTEMPORALIS) (Text-fig. 4)

The M. Pseudotemporalis arises on the posterior wall of the orbit from the alisphenoid below the fossa in the orbital wall. The site of attachment is separated laterally from the M. Adductor mandibulae posterior by a thin bony partition (see below), and mesially from the optic foramen by a similar partition. The muscle is tendinous throughout and it is attached to the ramus of the lower jaw in the mesial surface of the processus coronoideus. The site of attachment is a little below the antero-dorsal margin of the ramus anterior to the M. Adductor mandibulae posterior.

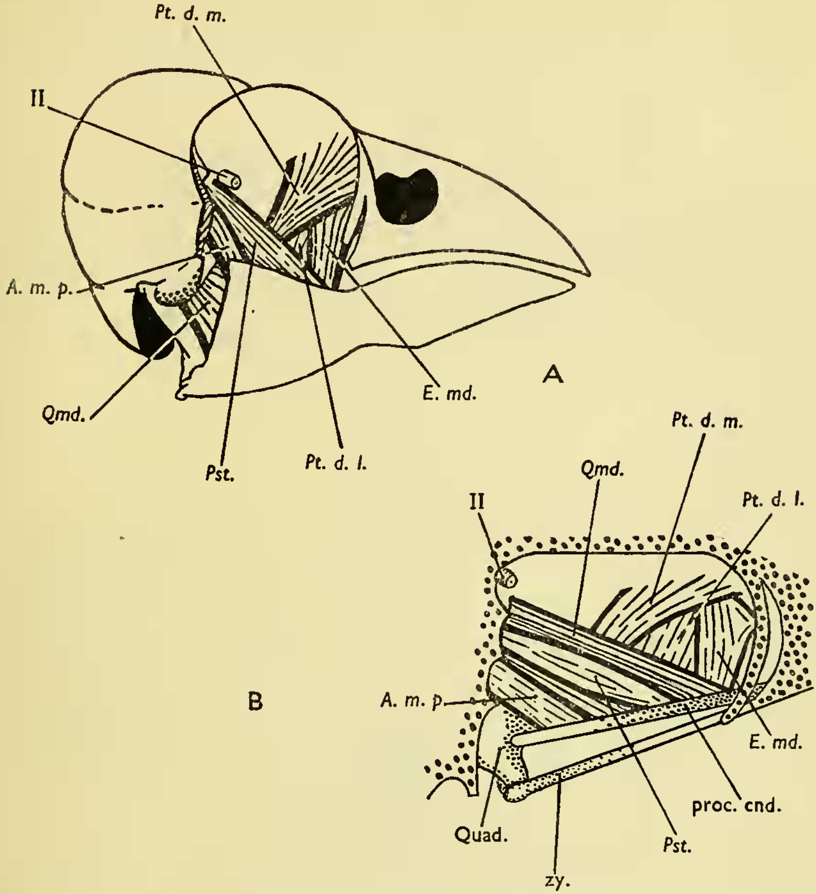

FIG. 4. ***Coccothraustes coccothraustes.*** A, Diagrammatic view of the right side of the head, eye and eye muscles removed to expose the jaw muscles in the orbit. B, Diagrammatic dorsal view of the right orbit. *A.m.p.*, M. Adductor mandibulae posterior; *E. md.*, M. Ethmo-mandibularis; *Pst.*, M. Pseudotemporalis (M. Adductor mandibulae internus); *Pt.d.l.*, M. Pterygoideus dorsalis lateralis; *Pt.d.m.*, M. Pterygoideus dorsalis medialis; *Qmd.*, M. Quadrato-mandibularis; *II*, Optic nerve.

M. QUADRATO-MANDIBULARIS (Text-fig. 4)

The M. Quadrato-mandibularis forms a thin sheet of muscle, almost devoid of tendinous tissue, underlying the Ms. Pseudotemporalis and Adductor mandibulae posterior. It extends from the quadrate to the mesial surface of the processus coronoideus. The muscle arises from both surfaces of the orbital process and as far as the neck of the quadrate where part of the pars profunda of the M. Adductor mandibulae externus originates. The muscle is inserted obliquely in the ramus of the lower jaw along a line tending to pass from below the site of insertion of the M. Pseudotemporalis towards the point of articulation with the quadrate.

M. ETHMO-MANDIBULARIS (Text-fig. 5)

The M. Ethmo-mandibularis arises from the anterior part of the interorbital septum above the palatine and partly from the anterior wall of the orbit, that is, from the mesethmoid. Some of the dorsal fibres pass horizontally across the anterior angle of the orbit and assist in the support of the main fibres which pass obliquely downwards and outwards back to that part of the lower jaw behind the gape. The fibres become tendinous a little before being inserted into the mesial surface of the ramus of the lower jaw above the ventral margin.

M. PTERYGOIDEUS (Text-fig. 5)

M. Pterygoideus dorsalis

M. Pterygoideus dorsalis medialis

The M. Pterygoideus dorsalis medialis arises from the interorbital septum at the antero-dorsal angle of the orbital wall above the attachment of the posterior part of the M. Ethmo-mandibularis. The muscle has numerous tendinous fibres near its site of origin, and these increase in number until the muscle is completely tendinous a little before the site of insertion. The muscle passes backwards and downwards between the ventral surface of the orbital process of the quadrate and the dorsal surface of the pterygoid (beneath the M. Protractor pterygoidei, see below). The muscle is attached by a very strong tendon to the ramus of the lower jaw at the head of the processus mandibulae internus. The tendon lies over the head of the inflexion and is inserted into the upper part of the posterior surface.

M. Pterygoideus dorsalis lateralis

The M. Pterygoideus dorsalis lateralis arises principally from the palatine and from the flattened area at the union of the pterygoid and the palatine. The thick fleshy fibres pass obliquely downwards and backwards and outwards to the site of insertion which is towards the ventral margin of the mesial surface of the ramus of the lower jaw, posterior to the M. Ethmo-mandibularis. The only tendinous tissue in the muscle is in the nature of a thin sheet extending throughout the entire muscle.

M. Pterygoideus ventralis

M. Pterygoideus ventralis medialis

The M. Pterygoideus ventralis medialis arises from near the top of the mesial surface of the processus mandibulae internus. It is a slender muscle and the fibres pass forwards and upwards becoming more tendinous. The tendon is inserted in the palatine along the outer (ventral) surface of the posterior process where it curves as if to meet the other member of the pair.

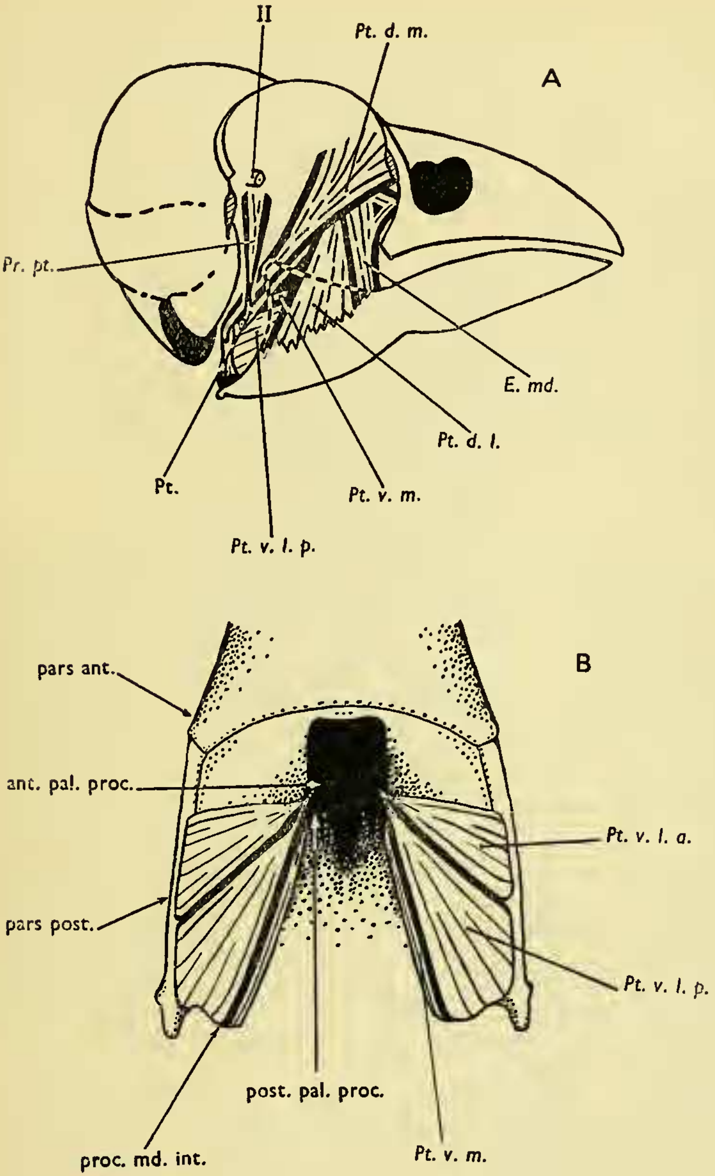

Fig. 5. ***Coccothraustes coccothraustes.*** A, Diagrammatic view of the right side of the head dissected to expose the ventral jaw muscles. B, Diagrammatic ventral view of the ventral jaw muscles. *Pr.pt.*, M. Protractor pterygoidei; *Pt.v.l.a.*, anterior portion of the M. Pterygoideus ventralis lateralis; *Pt.v.l.p.*, posterior portion of the M. Ptergoideus ventralis lateralis; *Pt.v.m.*, M. Pterygoideus ventralis medialis.

M. Pterygoideus ventralis lateralis

Anterior Portion. The anterior portion of the M. Pterygoideus ventralis lateralis is a thin fan-like muscle arising mainly from the ventral margin and partly from the mesial surface of the ramus of the lower jaw. The site of attachment is mid-way along the ventral margin of the pars posterior of the ramus. The fibres pass upwards mesially to other muscles, then they become more tendinous and are inserted along the outer member of the bifurcation at the distal end of the anterior palatine process.

Posterior Portion. The posterior portion of the M. Pterygoideus ventralis lateralis is a stouter muscle than the anterior portion. It arises along most of the mesial surface of the processus mandibulae internus of the lower jaw, that is, all of the mesial surface except for the small area occupied by the M. Pterygoideus ventralis medialis. It is also attached along a little of the ventral margin and mesial surface of the main body of the ramus of the lower jaw. The fibres are markedly tendinous and ultimately form a tough tendon which in inserted along the inner branch of the bifurcation at the distal end of the anterior palatine process (the anterior portion is attached to the outer branch).

Remarks on the Adductor Group

The relatively large area of attachment of the muscles of the Adductor Group indicates that the total stress of the combined contraction is evenly distributed over most of the cranium. The M. Adductor mandibulae externus arises over the lateral, dorsal, and posterior surfaces of the cranium and the Ms. Adductor mandibulae posterior and internus (M. Pseudotemporalis) arise over the anterior of the cranium, that is, the posterior wall of the orbit. The Ms. Pterygoideus and Ethmo-mandibularis are attached to the mesethmoid, palatine and the pterygoid and the stress of their contraction is relayed to the antero-ventral surface of the cranium by the interorbital septum.

Functionally, it is not strictly correct to include all the elements of the M. Pterygoideus in the Adductor Group of muscles, for when both the mesial members of the M. Pterygoideus dorsalis and ventralis contract they seem to assist in the depression of the lower jaw ; they draw the processus mandibulae internus of the articular forwards, and so rotate the anterior of the lower jaw downwards through the same angle (Text fig. 6). However, on closer examination it becomes apparent that these muscles and the posterior portion of the M. Pterygoideus ventralis lateralis hold the articulatory surfaces of the lower jaw and the quadrate in contact. Thus they strengthen the hinge mechanism and help prevent the dislocation of the jaw when the powerful crushing muscles contract.

If the upper mandible of *C. coccothraustes* were hinged and the palatines were free and formed part of this mechanism then those members of the Ms. Pterygoideus dorsalis and ventralis which are inserted in the palatines would act as *retractor* muscles. These would draw the palatines backwards so lowering the upper mandible and holding it fast. However, it seems proper to include all the members of the Ms. Pterygoideus dorsalis and ventralis in the Adductor Group for by their contractions they ensure the most efficient functioning of the main " adducting " muscles.

Not only is it valid to include these muscles in the same functional group because of their necessary simultaneous contractions but because they are innervated by the same branch of the trigeminal nerve.

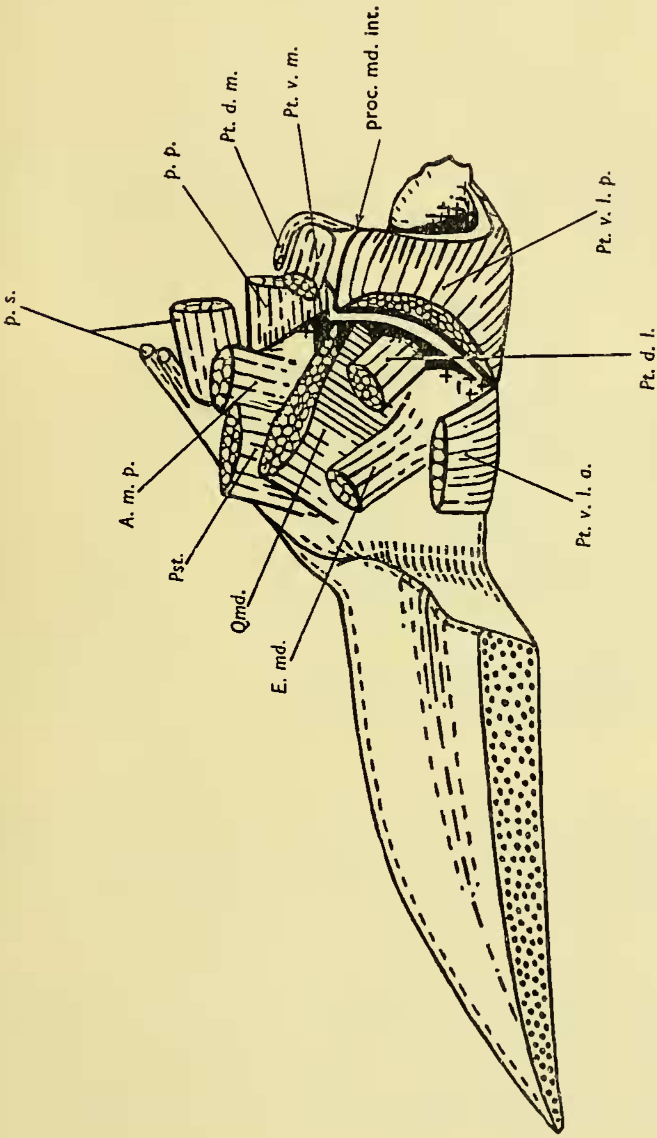

FIG. 6. *Coccothraustes coccothraustes.* Diagrammatic view from the left of the right sagittal half of the lower jaw showing the sites of origin or insertion of the jaw muscles over the mesial surface.

II The Constrictor "Group"

The depression of the lower jaw, as mentioned above, is effected by only one paired muscle.

Description of the Constrictor "Group"

M. DEPRESSOR MANDIBULAE (Text-figs. 3 and 7)

The M. Depressor mandibulae arises from the greater part of the exoccipital, especially the part forming the posterior wall of the bony meatus. The fibres of the muscle pass downwards without converging, or becoming very tendinous, to where they are inserted into the post-articular part of the mandible. Tendinous

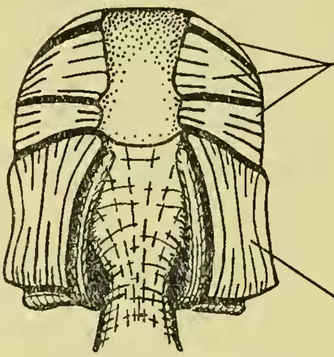

Fig. 7. ***Coccothraustes coccothraustes.*** Diagrammatic posterior view of the head showing the external jaw muscles.

insertions are made in the angular behind the lateral process, ventrally in the posterior of the angular, and in the posterior of the processus mandibulae internus. The fibres form a flat muscle which completely covers the mandibular articulation from behind and also forms a fleshy extension to the posterior wall of the meatus.

Remarks on the Constrictor "Group"

The M. Depressor mandibulae is a feeble muscle in comparison with the muscles of the Adductor Group. Its action does not necessitate any rapid contraction, nor is it required to exert any great force to depress the lower jaw. The chief function of the muscle is to overcome the effect of the relaxed, but unextended, muscles of the Adductor Group that would otherwise tend to oppose the depression of the lower jaw.

III The Protractor "Group"

The upper mandible does not articulate on the cranium in *C. coccothraustes* but although this mechanism is absent one functionless paired muscle, as already mentioned, persists as a vestigial structure.

Description of the Protractor "Group"

M. PROTRACTOR PTERYGOIDEI (Text-fig. 5)

The M. Protractor pterygoidei is a slender muscle arising from the alisphenoid in the posterior wall of the orbit a little below the optic foramen. The fibres pass downwards and outwards beneath the orbital process of the quadrate ; they converge and becoming tendinous are attached to a small dorsally situated spine-like process near the quadratal end of the pterygoid.

Remarks on the Protractor "Group"

In species where the upper mandible is hinged on the cranium the function of the M. Protractor pterygoidei is to draw the distal (quadratal) end of the pterygoid upwards. The quadrate is attached to this and when the pterygoid moves upwards the quadrate is rotated forward, thrusting the pterygoid forward at the same time. This action pushes forward the palatine under the interorbital septum. The upper mandible is hinged to the cranium on the dorsal side so that forward movement on the ventral side communicated by the palatines has the effect of lifting the bill on its hinge. The zygoma is also attached to the quadrate and the forward rotation of the quadrate causes the zygoma to be moved forward, thus assisting in the elevation of the upper mandible since the zygoma is joined to the maxilla. Although the muscle is functionless in *C. coccothraustes* is is interesting to note that its fibres are not completely lacking in tendinous strands and generally the muscle closely resembles the form of the muscles of the Adductor Group.

COMPARATIVE NOTE

For comparative purposes the Chaffinch, *Fringilla coelebs*, and the Brambling, *F. montifringilla*, have been selected as more generalized fringilline species.

In comparison with *C. coccothraustes* the oral surfaces of the rhamphotheca of *F. coclebs* are smooth and lack any dilations similar to the striated pads, or bosses (Text-fig. 8*b*). It would appear (Sushkin, 1925) that this specialization is not confined to *C. coccothraustes* for apart from *Hesperiphona* of North America the occurrence of specializations of this nature are found in a few other Old World genera, namely, *Eophona*, *Perissospiza* and *Mycerobas*.

In comparison with the skull of *C. coccothraustes* that of *F. coelebs* is a fragile structure and this difference is illustrated by comparing the sizes and the weights of the skulls of the two species. The average maximum dimensions of skulls of *C. coccothraustes* are 40 × 20 × 20 mm. and *F. coelebs* 30 × 14 × 15 mm. ; if the cube of each of the linear proportions of the skull of *C. coccothraustes* is compared with those of a hypothetical skull of the same average dimensions as *F. coelebs*, but of the *same design* as that of *C. coccothraustes*, it is found that the dimensions of the skull of *C. coccothraustes* average 250% " larger ". Yet the average weights of the skulls of *C. coccothraustes* and *F. coelebs* are 3·235 gm. and 0·654 gm. respectively, that is, the skull of *C. coccothraustes* contains nearly 400% more bony material than that of *F. coelebs*. Therefore, the skull of *C. coccothraustes* is very massive for its size.

The outline of the skull of *C. coccothraustes* has been likened to one horn of a crescent, but the skull of *F. coelebs* differs by being more cuneiform, and its dorsal profile is nearly straight (Text-fig. 8*a*). The difference is attributable mainly to the

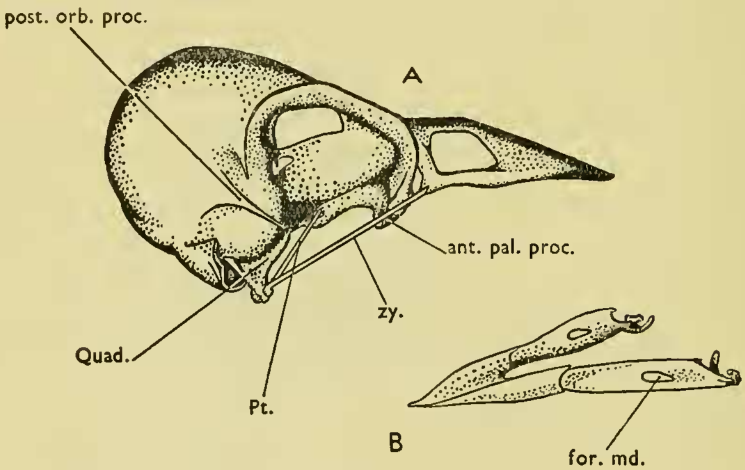

Fig. 8. ***Fringilla coelebs.*** A, Cranium and upper jaw lateral view from the right side (compare Text-fig. 2*a*). B, Lower jaw (compare Text-fig. 2*b*).

greater angle between the basi-cranial and basi-maxillary axes[1] in *F. coelebs* which is 150° but only 120° in *C. coccothraustes.*

Van der Klaauw and Duijm consider that a difference of this nature can be a functional adaptation and Duijm stated, " . . . the bill and the cerebral capsule behave mainly as independent functional elements.". In the present instance the downward rotation of the bill relative to the cranium in *C. coccothraustes* reduces some of the stresses set up by the application of powerful forces to crack fruit stones. This is shown diagrammatically in fig. 9. Here BC and AB represent the basi-maxillary axis and a line parallel to the basi-cranial axis in two skulls of the same overall length. In (A) the subtended angle between the two is 120° as in *C. cocco-*

[1] Basi-maxillary axis: The line of intersection between the vertical longitudinal plane of the head and the mean ventral surface of the premaxillae.

thraustes, and in (B) it is 150° as in *F. coelebs*. Assuming that the same forces were applied to the lower jaw to crack a nut held at the same distance from the angle of the jaw, then the magnitude and direction of the force, relative to the upper jaw, can be represented as the line XY. The direction of the force is tangential to a circle whose centre is at the articulation of the lower jaw, A, and periphery at D, where the lower mandible presses against the stone. The force XY is resolvable into two

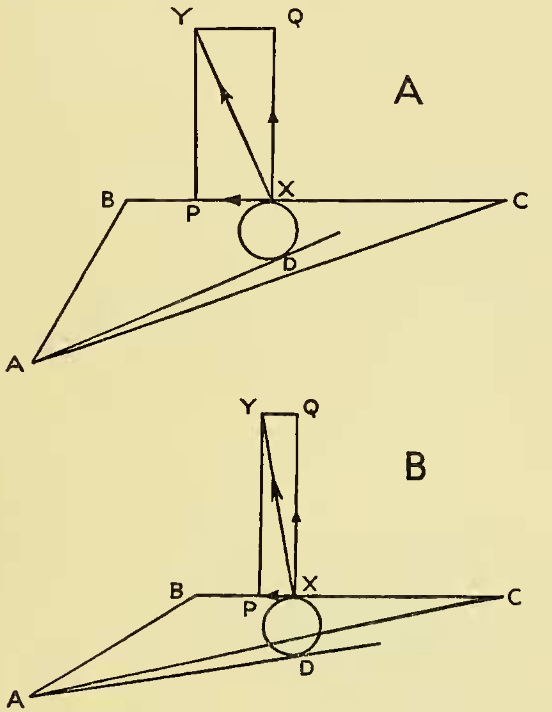

FIG. 9. Diagram showing the main forces imposed on the upper jaw when food is crushed between the mandibles. A, The subtended angle, ABC, between the basi-maxillary and basi-cranial axes is 120°. B, The subtended angle is 150°.

components at right angles to one another, XP and XQ. The former exerts a compressional and the latter a bending strain on the upper jaw. A bending strain is clearly more likely to fracture the bill than a compressional strain along its length and the bending component is approximately 6% less in (A) where the angle between bill and cranium is similar to that of *C. coccothraustes*. Therefore, the downward rotation of the bill in *C. coccothraustes* may be regarded as an adaptation to feeding so that hard stones are cracked with a smaller bending strain being experienced by the bill; that is, there is less chance of fracture than in a skull of the design of *F. coelebs* where the subtended angle between the bill and cranium is more obtuse.

The bending strain which is experienced by the bill of *C. coccothraustes* when fruit stones are cracked must nevertheless still be relatively enormous when forces in the region of 100 lb. have to be applied to crack them, but its effect is largely nullified by the highly ossified septa. These are markedly different in *F. coelcbs* where the interorbital septum exhibits a more normal passerine condition forming only a thin bony partition between the orbits and the nasal septum appears to be mainly unossified.

Again, a high degree of ossification is found in the pterygoid-quadrate-zygoma system, for in comparison the pterygoids and zygomae of *F. coelebs* are long and slender, while the quadrates of *C. coccothraustes* are about twice the size of those of *F. coelebs*.[1]

An examination of the skulls reveals that not only has the skull of *C. coccothraustes* become modified to withstand greater stress, but also to provide a greater area of the attachment and insertion of the jaw muscles. This latter point is well illustrated by the difference observed between the lower jaw of *C. coccothraustes* and *F. coelebs*. In the former the coronoid is elevated in correlation with the large size of the pars medius of the M. Adductor mandibulae externus which is inserted into it, moreover, the foramen mandibularis is very small while it is relatively large in *F. coelebs* (Text-fig. 10). The disparity in the sizes of the partes medii in the two birds is

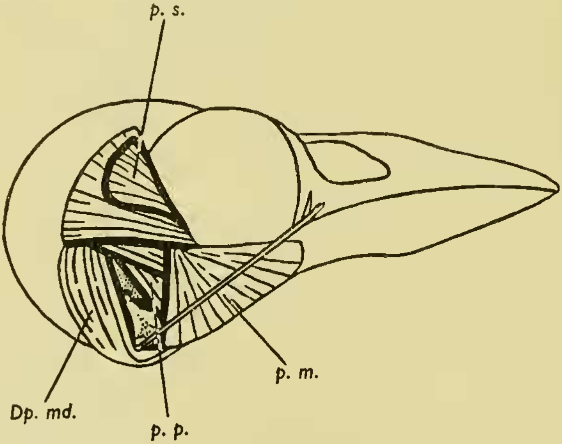

FIG. 10. ***Fringilla montifringilla.*** Diagrammatic view of the right side of the head showing the external jaw muscles (compare Text-fig. 3).

also reflected in the degree of development of the respective post-orbital processes of the squamosals from which they originate. Generally the lower jaw of *F. coelebs* appears to be more primitive in character than that of *C. coccothraustes* which, in addition to the adaptations just referred to, is modified to carry the heavy bosses of the bill, as described above.

[1] Quadrate of *C. coccothraustes :* mass 0·0375 gm., 9 mm. high × 7 mm. long (orb. proc.). Quadrate of *F. coelebs :* mass 0·0041 gm., 4·5 mm. high × 4·5 mm (orb. proc.).

The jaw muscles of *C. coccothraustes* in comparison with those of the Brambling, *Fringilla montifringilla*, are exceedingly tendinous. In the latter they are composed of fleshy fibres almost devoid of tendons, except at the site of insertion, and even then the tendons are not as evident as those in *C. coccothraustes*. The jaw muscles of *F. montifringilla* are generally more bulky and appear to contain much non-contractile tissue. One gains the impression that the flaccid muscles of *F. montifringilla* are incapable of the rapid powerful contractions of the muscles of *C. coccothraustes*.

The difference in the form of the M. Adductor mandibulae internus (M. Pseudotemporalis) in the two species illustrates the comparatively compact nature of the muscles of *C. coccothraustes*. In this bird the M. pseudotemporalis is squarish in cross-section and extends from the posterior wall of the orbit to the lower jaw. In *F. montifringilla*, on the other hand, the M. pseudotemporalis although similarly attached and inserted forms a fleshy floor to the orbit filling the spaces between the Ms. Adductor mandibulae posterior, Pterygoideus dorsalis and Ethmo-mandibularis. Yet, despite its size, the muscle probably does not contract with the same forces as its smaller counterpart in *C. coccothraustes*.

The nature of the jaw muscles in *C. coccothraustes* is not the only factor contributing to a powerful musculature, but their size and distribution are also important. A comparison of the relative sizes and the areas of attachment of the various portions of the M. Adductor mandibular externus illustrates this point. It can be seen (Text-figs. 3 and 10) that the area of attachment of this muscle in *C. coccothraustes* is disproportionately greater than in *F. montifringila*. In *C. coccothraustes* the muscle arises from over most of the external surface of the cranium whereas in *F. montifringilla* the areas of attachment are confined to the lateral and postero-lateral surfaces.

The essential difference between the myology of the jaw of *C. coccothraustes* and that of *F. montifringilla* appears to be one of degree, that is, area of attachment and tendinosity. However, what I have termed the "anterior portion" of the M. Pterygoideus ventralis lateralis appears to be absent in *F. montifringilla*. In this species the M. Ethmo-mandibularis is more prominent and its site of origin extends over the comparable area of origin of the anterior portion of the M. Pterygoideus ventralis lateralis in *C. coccothraustes*. It would appear from this that the M. Ethmo-mandibularis is divided into two parts in *C. coccothraustes*. However, since in *C. coccothraustes* the anterior portion is inserted into the palatine along with the posterior portion of the M. Pterygoideus ventralis lateralis I am of the opinion that the anterior portion should be considered as a part of the M. Pterygoideus ventralis lateralis, and this seems justifiable since the portions are also functionally complementary.

DISCUSSION

The purpose of this paper has been to indicate some of the modifications in the morphology of the head of *C. coccothraustes* which appear to be related to its ability to crack open various fruit stones, such as those of the cherry, damson and olive. There are, however, several points requiring further investigation.

There is, for example, a point of interest in the development of the horny pads of the rhamphotheca. It seems that these pads, or bosses, do not appear until the bird reaches maturity. In the limited sample examined they were not found in nestlings nor in birds in immature plumage. Even if pads were present in young birds they would be non-functional because from an examination of the stomach contents it appears that the adults are primarily insectivorous during the breeding season (Mountfort, in press) which indicates that the nestlings are fed mainly on insects. Similarly, the pads are not required by immature birds because they have been observed to feed on caterpillars, especially the Hornbeam caterpillar, *Carpinus betulus*.

The appearance of the horny pads late in the development of the individual could be interpreted as evidence that the structures have been acquired recently in the history of the species. However attractive this argument may appear to be at first sight it is misleading because the pads should not be considered apart from the associated osteological and myological modifications ; and it is possible that if the pads were present in an immature bird they would even be a danger to it ! One of the chief characteristics of young passerine birds is the absence of osseous material in most of the cranium and the slow rate at which ossification occurs as the young bird matures. The absence of osseous material makes the skull extremely fragile, the more so since the sutures between the bones remain open almost until maturity. The skull of a young bird is, therefore, not strong enough either to wishstand the stresses of cracking open fruit-stone kernals or to accomodate the powerful musculature capable of closing the jaws with a force in the region of 100 pounds, that is if the muscles could be precociously developed to contract with that force. It seems, therefore, that the late development of the pads cannot be regarded as indicative of their appearance in the phylogeny of the bird.

CONCLUSIONS

The structural modifications which have occurred in the head of *C. coccothraustes* and enable the bird to apply and withstand a force in the region of 100 lb. are profound. It appears that no part of the head, which has been considered, has escaped specialization. The oral surfaces of the horny bill are modified and equipped with striated pads between which the food is gripped. The skull, particularly the upper and lower mandibles, is strengthened to withstand the stress of cracking a hard fruit stone and it is modified to accommodate the powerful musculature of the jaw as well as to withstand the force of the contraction of the muscles. The musculature of the head is highly developed with large areas of attachment, and the individual muscles are tendinous in nature and powerful in action.

The possession of these modifications are undoubtedly a selective advantage to the bird particularly during the period of great increases in population which partly coincides with the " soft-fruit " season. *C. coccothraustes* comes less into competition with other seed-eaters and its own young at an important time of the year by utilizing fruit-stones and similar large seeds, berries and, during the breeding season, large insects.

APPENDIX

Crushing Tests on Cherry and Olive Stones

(*a*) The National Physical Laboratory carried out a series of crushing tests and made the following report:

The apparatus used for the tests was designed to simulate, as far as possible, the mandibles and pressure pads of this bird. It consisted of a steel compression rig with two ¼-in. diameter rods which fitted into two deep grooves in the lower block of the apparatus, and a flat serrated cross piece attached to the upper block. The bare fruit stone was placed between these loading points and cracked; the load being increased by moving a jockey weight along the lever of the testing machine. The time taken to crack each stone was approximately 20 seconds.

In order to represent the influence of the direction of the seam or suture of the stone in the bird's beak, the tests were made with the seam facing several directions.

The results of the tests are given in Tables I and II.

(*b*) Mr. D. B. Welbourne, of the Department of Engineering, Cambridge, working independently obtained comparable values when he crushed cherry stones in a Housefield Tensometer. In correspondence, he writes, that in his tests he effected different rates of loading and found that more rapid loading resulted in higher failure loads, that is, a greater pressure is required to break a stone quickly than to break it slowly. Therefore, the crushing loads given in Tables I and II should not be regarded as the maximum pressures applied by *C. coccothraustes* when cracking fruit stones; for the values, determined by the tests, were obtained in each case by applying the pressure for approximately 20 sec. which is a greater time than it takes *C. coccothraustes* to crack a fruit stone.

TABLE I.—*Crushing tests on Cherry Stones*

Test	*Direction of seam*	*Type of Cherry*	*Crushing load* (lb.)
1	Sideways	Dark	64
2	,,	,,	62
3	,,	,,	70
4	,,	,,	62
5	Upwards	,,	70
6	,,	,,	65
7	Downwards	,,	61
8	,,	,,	60
9	,,	,,	62
10	,,	,,	65
1	Sideways	Light	95
2	,,	,,	93
3	Upwards	,,	70
4	,,	,,	68
5	,,	,,	70

TABLE II.—*Crushing tests on fresh Olive Stones*

Test	*Direction of seam*	*Type of stone*	*Crushing load* (lb.)
1	Sideways	Olive	111
2	,,	,,	110
3	,,	,,	106
4	,,	,,	114
5	Upwards	,,	125
6	,,	,,	137
7	,,	,,	147
8	,,	,,	143
9	Downwards	,,	136
10	,,	,,	107
11	,,	,,	138
12	,,	,,	159

Physic's Division.
National Physical Laboratory.

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